ENVIRONMENTAL INTERACTION IN SUMMER ALGAL COMMUNITIES OF UTAH LAKE[1]

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Abstract.— Utah Lake is a shallow eutrophic lake in central Utah. It is characterized by high nutrient and silt loads and by large algal blooms in late summer and early fall. Phytoplankton samples and environmental data were taken from June through August 1974. Phytoplankton species were identified and then quantified in a Palmer counting cell. Environmental continuum theory was employed to describe algal succession, and regression analysis was used to discover interactions between algal communities and the environment. Phytoplankton communities in June were characterized by high species diversity. As the lake environment became stressed in late summer due to higher turbidity, nutrient levels, pH, and available inorganic carbon species diversity decreased. By August, the phytoplankton flora was composed essentially of only two species, *Ceratium hirundinella* and *Aphanizomenon flos-aquae*.

Utah Lake is a shallow eutrophic lake in central Utah (Fig. 1). It is the largest naturally occurring freshwater lake in the state, covering some 388 km^2 (Bolland 1974). Water from the lake is presently used for irrigation and water regulation as well as for recreational boating and fishing.

In the past, commercial fisheries on Utah Lake have been an important resource for the state of Utah. At the time of settlement, the fish population was dominated by a variety of Bonneville cutthroat trout (*Salmo clarki*) which was adapted to the eutrophic conditions of the lake. The trout fishery became vital to the survival of the early Mormon pioneers during the drought and crop failures from 1855 to 1858. However, with water manipulation for agriculture and the introduction of exotic fish species, the trout rapidly became extinct in subsequent years. During the depression years of 1929 through 1939 commercial fishing for introduced species, mainly carp and white bass, became an important industry and food source. Current use of Utah Lake fisheries is minimal and limited to carp, which are used for fish meal.

Utah Lake is characterized by late summer and early fall algal blooms, nutrient enrichment, high silt load, and total dissolved solids and other environmental stresses. Due to the shallowness of the lake (average depth 2.4 m), fine silt-clay sediments are often stirred up by storms, giving the lake water a characteristic gray-green color. The average summer Secchi disk reading is 24 cm, with a range of 12 to 50 cm. In addition, the lake basin receives the flow of numerous mineral springs high in carbonates and sulfates.

During late summer, when water levels are lowest, the lake approaches a slightly saline ecosystem. According to the U.S. Geological Survey (Hem 1970), lakes with 1,000-3,000 mg/liter dissolved solids can be considered to be slightly saline. Summer values for dissolved solids in Utah Lake range from 795 to 1,650 mg/l and are thus in the lower part of this range.

Previous algal studies of Utah Lake were done by Tanner (1930, 1931), Snow (1932), Harding (1970, 1971), and Bolland (1974). Tanner's pioneering works listed several of the algae prominent in the lake. Both Harding and Snow did taxonomic studies dealing with littoral and planktonic algae. Bolland's work dealt with the fossil diatom flora in the lake sediments. Bolland's research indicates that the diatom flora has not changed greatly since presettlement times.

Data for this study were gathered during

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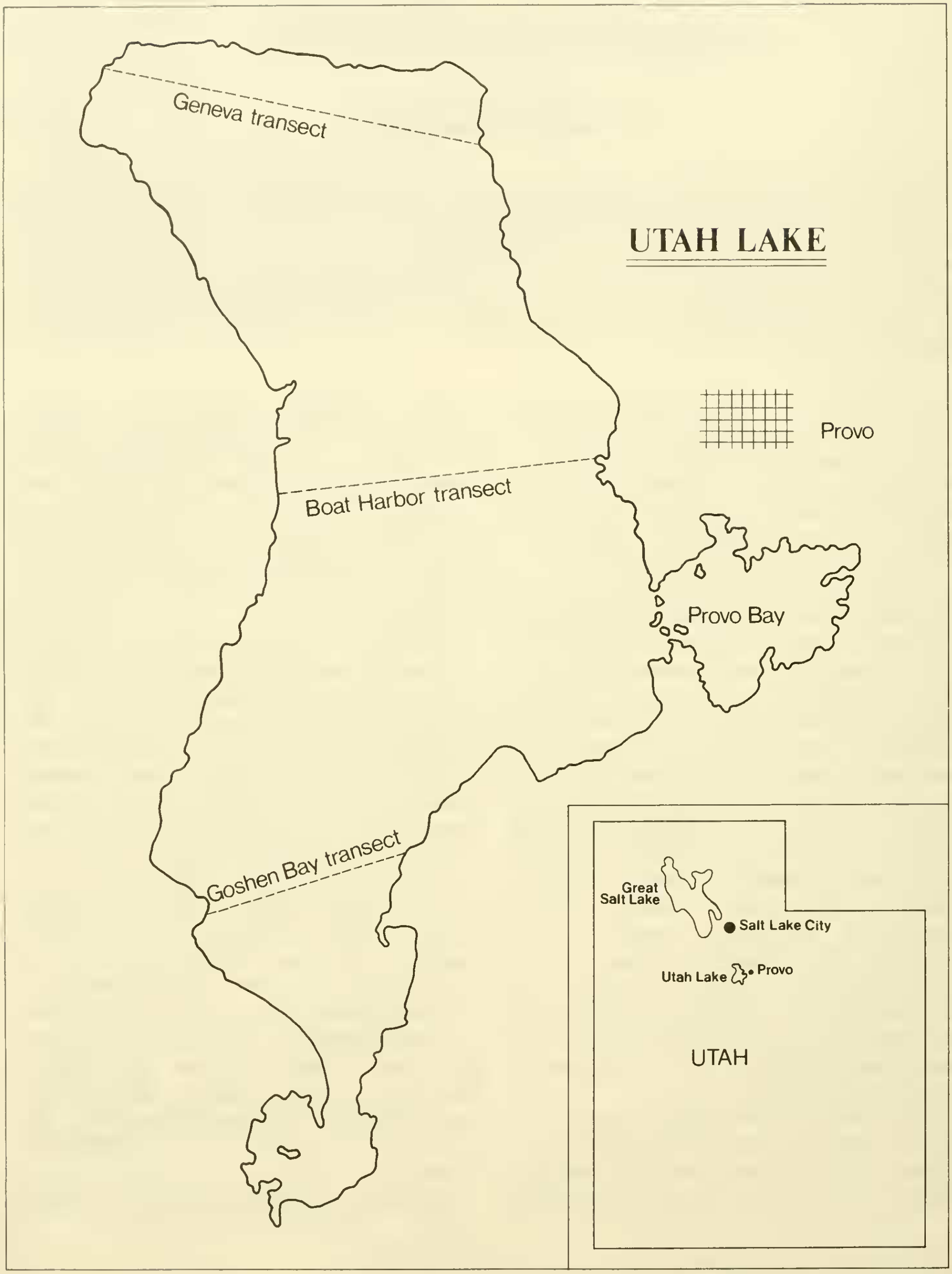

Fig. 1. Utah Lake, showing geographical position with respect to the state of Utah, Provo, and the Great Salt Lake.

the summer of 1974. There had been no previous quantitative study of the extant planktonic flora. The study resulted in a floristic paper (Rushforth et al., in press) as well as estimates of productivity and a description of the seasonal succession of summer algal species in Utah Lake to be reported herein.

Methods

Phytoplankton samples and environmental data were collected from June to August 1974. Samples were taken along three transects at nine-day intervals throughout the study period. The transects (Fig. 1) included 14 sample sites permanently marked with buoys. Transects were chosen to cross three major portions of the lake, each with possible differences in ecological conditions. The Geneva transect crossed the northern part of the lake from the outfall of the settling ponds of Geneva Works of the United States Steel Corporation to the western shore. The midlake transect ran west from the Provo Boat Harbor (near the mouth of the Provo River) to the west shore. The southern transect crossed Goshen Bay from Lincoln Beach to the west shore. The Geneva and Boat Harbor transects included five sampling sites, and the shorter Goshen transect had four sampling sites.

Phytoplankton samples were collected by pouring known volumes of lake water through a 67-μm mesh plankton net. Algae were washed from the net, collected in 30-ml vials, and immediately preserved in formalinacetic acid (FAA). The vials were later subsampled in the laboratory and individual algae were counted in Palmer counting cells (Palmer and Maloney 1954) at 400X magnification, using Zeiss RA research microscopes. Individual algae encountered were identified to the species level by two of us (Whiting and Rushforth). An "individual" for filamentous or colonial forms was considered to be a single filament or colony. Tallies were made for each species, as well as for the total number of individuals per subsample. The density of organisms in the original lake water was calculated using multiplication factors determined by the volume of filtered lake water. At least 400 individuals were counted in each sample to reduce sample variance (Clark 1956).

Selected water chemistry tests were performed in the field using a Hach DR/EL-2 Direct Reading Engineer's Lab. Tests for dissolved oxygen, free carbon dioxide, pH, and Jackson Turbidity readings were performed. In addition, a YSI conductivity meter was used to measure salinity, conductivity, and water temperature. Secchi disk readings and general meterological conditions were also recorded.

Further water chemistry tests were performed in the laboratory. Water samples were collected in opaque Nalgene bottles from approximately 25 cm below the water surface and were refrigerated until analyzed. Laboratory analyses included total alkalinity, carbonate alkalinity, total hardness, calcium hardness, magnesium hardness, nitrate, orthosphosphate, sulfate, and silica. All tests were performed within 24 hours of collection, using standard methods (Taras 1971).

Changes in phytoplankton populations through the summer were evaluated, using the continuum methods of Curtis and McIntosh (1950, 1951). Continuum theory is an approach to vegetation and its response to environmental gradients. Continuum study involves the calculation of an index number for each sample which places that sample at some point along an environmental gradient. The index number is considered to reflect the effects of the total environment on a sample expressed in terms of the species composition and their relative abundance. To demonstrate succession, the gradient herein is generated as a time continuum.

To generate the continuum index numbers used, the average density (in numbers of organisms/liter) for each species was calculated for all sites on each sample date. Adaptation numbers assigned to each algal species reflect the date at which each achieved maximum abundance. The adaptation numbers ranged from 1 to 8, corresponding to eight sample dates beginning on 13 June 1974 and ending 15 August 1974. The adaptation numbers for all species present in any one sample were then summed and averaged. The average adaptation number (continuum index number) for a sample describes its position along the time continuum. Sample index values ranged from 1.58 to 7.00. No sample was found to contain exclusively early summer species or late summer species.

All sample index values were plotted along an axis representing the time continuum. The continuum was then divided into six "natural" groups of approximately equal length, utilizing naturally occurring breaks as nearly as possible. The six divisions of the continuum allowed averages of environmental and biotic parameters to be calculated for each unit. Such average values show the successional trends along the continuum. The parameters plotted included eight major algal species, nine significant environmental parameters, environmental variation (heterogeneity), community variation, and species diversity.

A similarity index matrix using environmental data for each stand in each unit of the continuum was constructed. Mean similarity indices and standard deviation values for each unit of the continuum were then computed. A coefficient of variation was then computed from these values (Gilmartin 1974). All data values were adjusted to range from one to 10 to avoid overweighting some parameters because of their large numerical values.

Community variation was measured as above, except the data utilized were taken from the relative densities of the species present. In this instance, community variation is considered to be a measure of the evenness of the contribution each species makes to a sample.

Species diversity was calculated, using the Shannon-Wiener formula, as follows:

$$D = -\Sigma p_i \log p_i$$

The term p_i refers to the portion of the sample that each species contributes. The Shannon-Wiener formula expresses diversity in terms of the number of species present as well as the evenness of the contribution that each species makes to the total sample.

The response of individual species to single environmental parameters was assessed using the linear regression analysis. Those species with significantly similar responses ($\alpha = 0.01$) to the same environmental parameters were grouped together into "clusters."

Results

A total of 107 phytoplankton and environmental samples were taken. Ninety-five species were identified and ranked by importance values (average relative density X average percent presence). The six most important species and their importance values were: *Ceratium hirundinella* (3,303), *Aphanizomenon flos-aquae* (1,725), *Melosira granulata* (1,255), *Microcystis protocystis* (252), *Anabaena spiroides* (249), and *Anabaena flos-aquae* (154) (Fig. 2).

The early summer flora can be characterized by low standing crop (an average of 11,260 ± 25,700 organisms/liter in June) and rich species diversity. The June communities were dominated by several species of green algae, including *Ankyra judayi*, *Schroederia setigeria*, *Treubaria triappendiculata*, *Dictyosphaerium ehrenbergii*, *Pediastrum duplex*, and three varieties of *Ankistrodesmus falcatus*. Associated with these chlorophytes were the blue-greens *Anabaena flos-aquae* and *Microcystis protocystis*, the diatom *Melosira granulata*, and the dinoflagellate *Ceratium hirundinella*.

By early July, the green algae as a group began to decline in importance and were replaced by *Melosira granulata*, *Ceratium hirundinella*, and *aphanizomenon flos-aquae* (Fig. 3). King (1970) and others have indicated that the green algae tend to require free CO_2 for maximum growth and are poor competitors for bicarbonate. Our evidence seems to corroborate this conclusion. Free CO_2 in Utah Lake declined to levels that were undetectable with Hach chemistry (Fig. 4) at the same time the green algae decreased in importance. The July standing crop averaged 329,425 ± 291,410 organisms/liter, almost 30 times the June average.

August phytoplankton communities were much reduced in species diversity, often consisting only of two species, *Ceratium hirundinella* and *Aphanizomenon flos-aquae*. These two taxa were usually 10-50 times

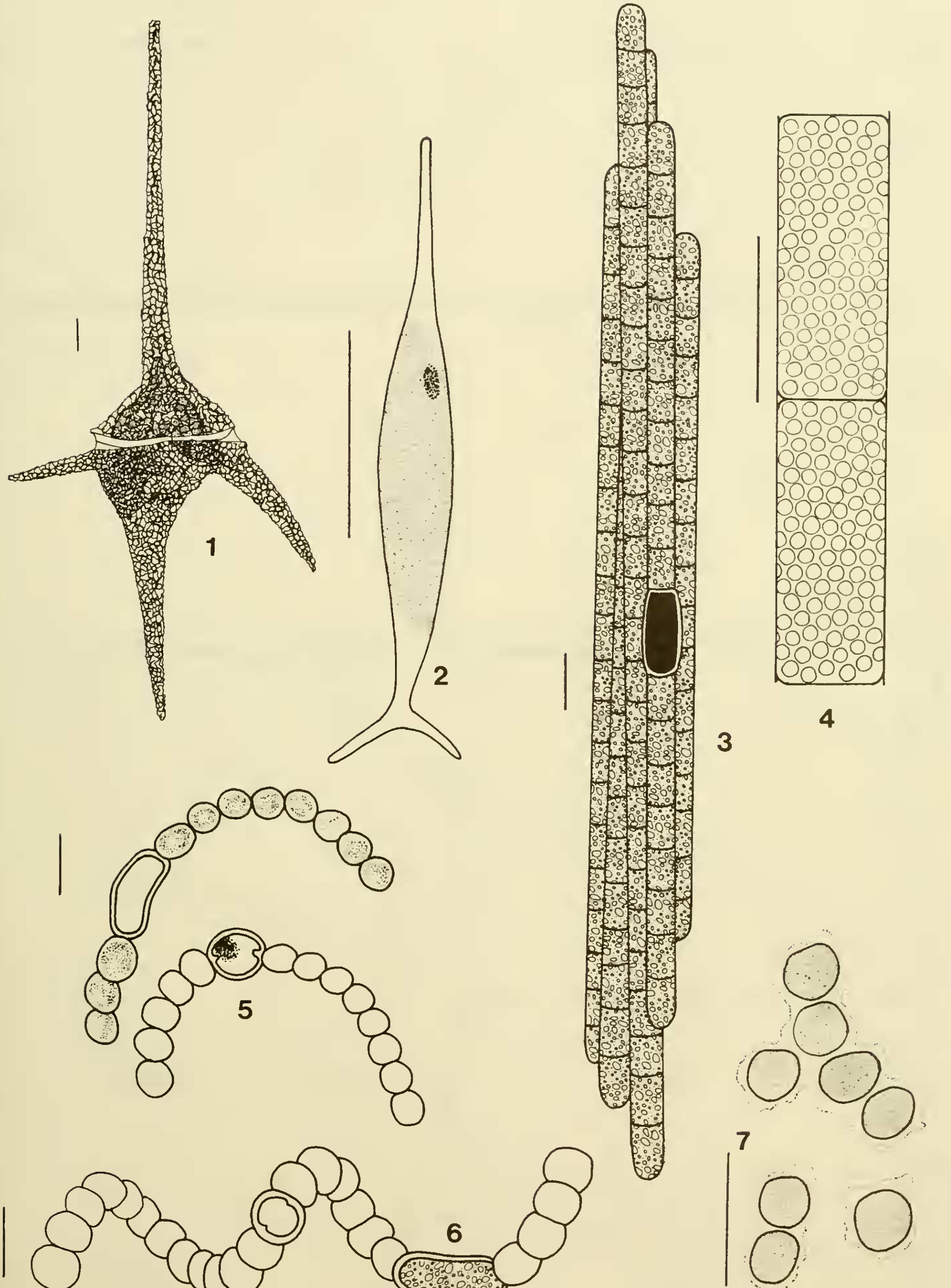

Fig. 2. Dominant phytoplankton species in the Summer Utah Lake flora. 1, *Ceratium hirundinella*; 2, *Ankyra judayi*; 3, *Aphanizomenon flos-aquae*; 4, *Melosira granulata*; 5, *Anabaena flos-aquae*; 6, *Anabaena spiroides*; 7, *Microcystis protocystis*. Each scale equals 10 μm.

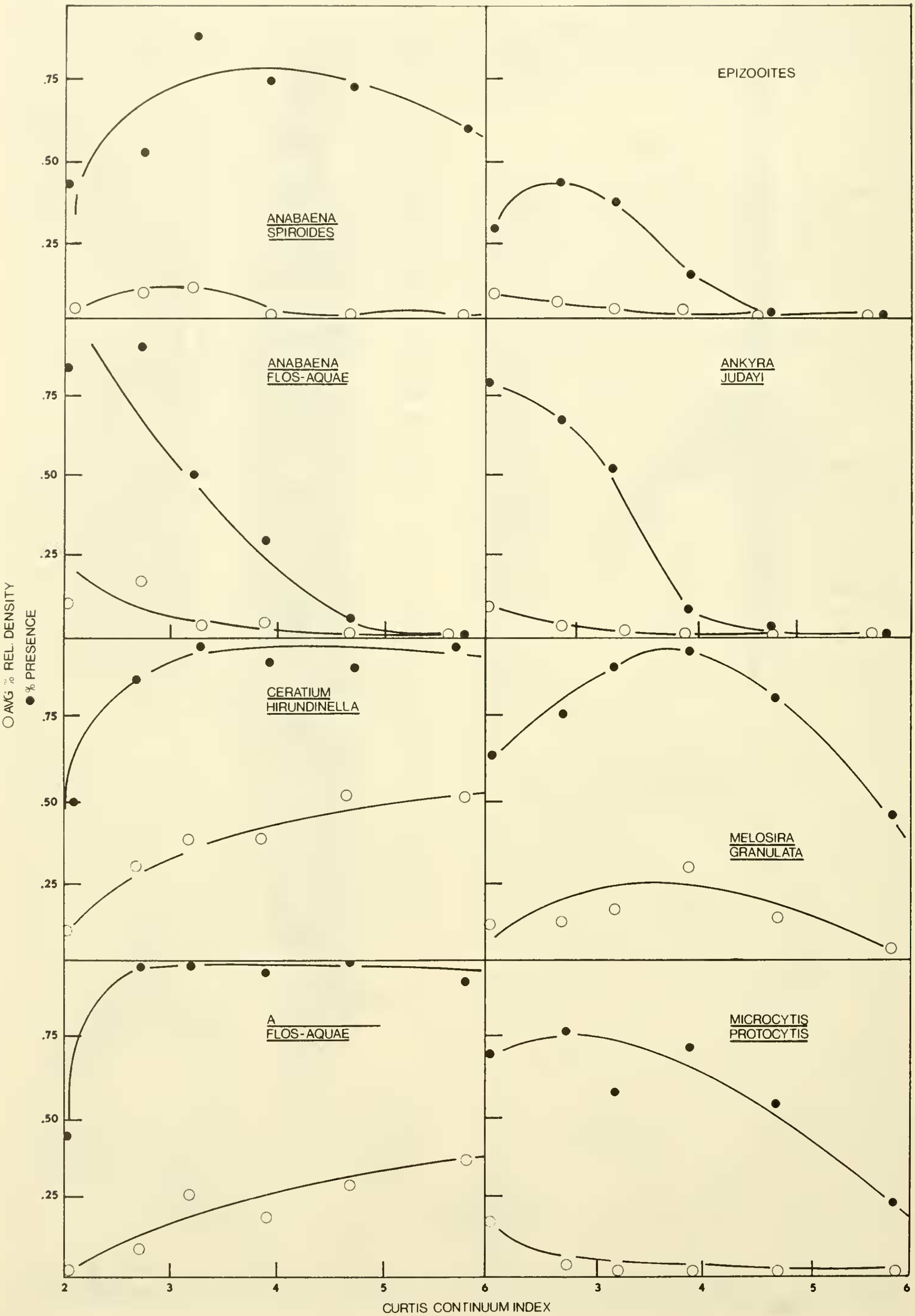

Fig. 3. Relative density and percent presence of common algal species in the Utah Lake summer 1974 flora plotted on the Curtis continuum index.

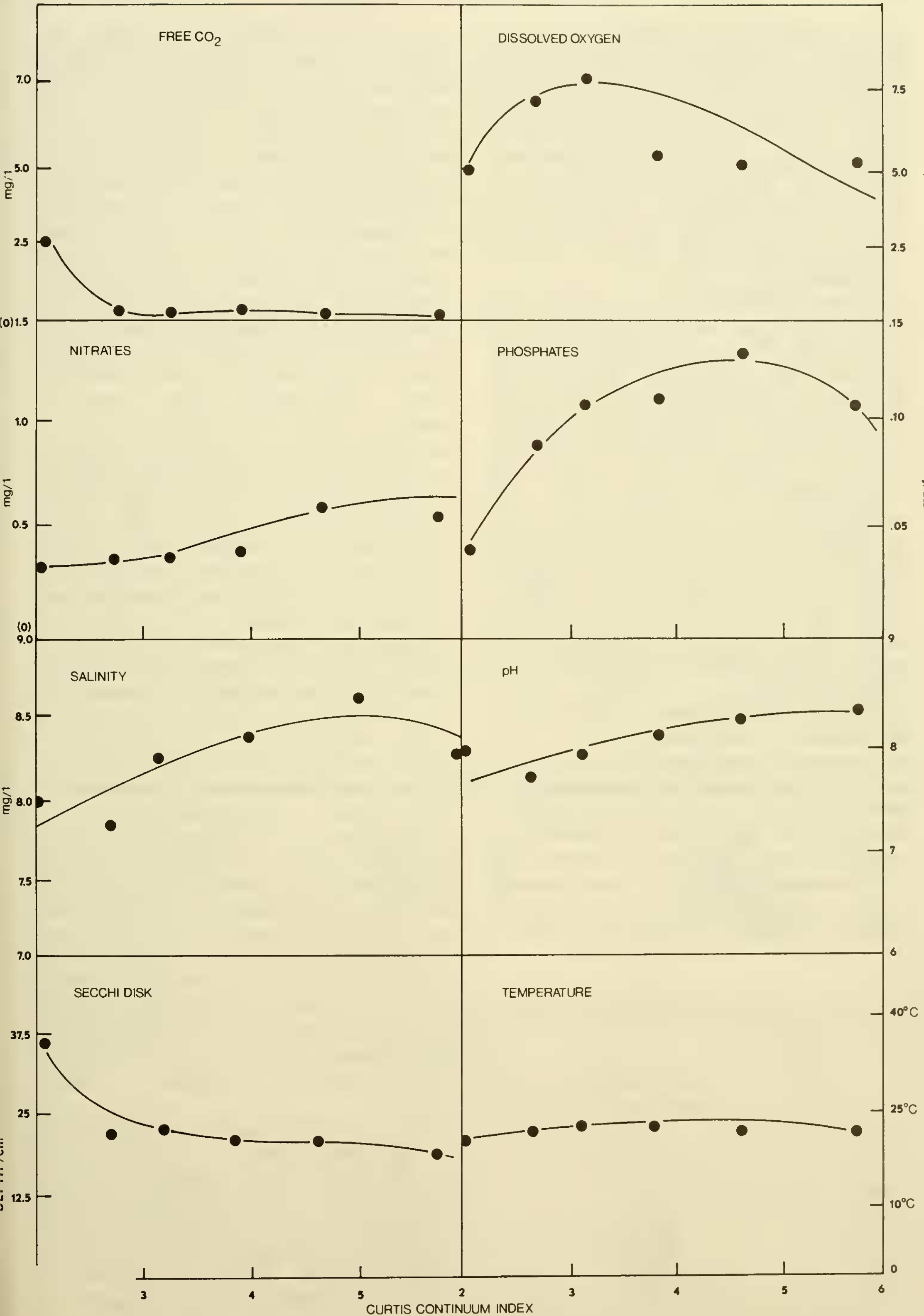

Fig. 4. Selected environmental gradients in Utah Lake in the summer of 1974, plotted on the Curtis continuum index.

more abundant than any other species. The decline in other species, especially *Melosira granulata*, might be attributed to any of a number of factors, such as decrease in availability of inorganic carbon, higher turbidity, higher salinity, or interspecific competition. The average estimate of the August standing crop was 5,405,226 ± 15,719,846 organisms/liter, almost 16 times the average for July and nearly 500 times the average for June (Table 1).

Biomass estimations for any given day showed large variation from one sample site to the next. This disjunct distribution was probably due to currents and possibly patchiness of the environment. George and Edwards (1973) have shown that zooplankton distribution is strongly correlated with Langmuir circulations. They demonstrated that *Daphnia* tend to aggregate in upwellings between foam lines. Presumably, phytoplankton may also be oriented in relation to Langmuir currents. Floating objects, such as blue-green algae with gas vacuoles, should aggregate in the foam lines. Other algae with well developed powers of locomotion might aggregate between foam lines as do zooplankton.

Analysis of phytoplankton using the Curtis continuum is summarized in Fig. 3. The six species with the highest importance values are plotted against the continuum. *Ankyra judayi* and "epizooites" (two unidentified species of Chrysophyta found on copepods) were also plotted. Although not very important overall, they were included because of their importance in the early summer. Generally, the continuum data indicate similar trends to those already described. The early summer phytoplankton consisted of a diverse group of diatoms, and green and blue-green algae. Although present from the beginning of the study, *Aphanizomenon*, *Ceratium*, and *Melosira* did not become abundant until July. *Melosira* showed its maximum growth around mid-July. *Aphanizomenon* and *Ceratium* continued to become more abundant until the end of the study in August, when they made up approximately 90 percent of the total flora.

Analysis of environmental parameters using the Curtis continuum is summarized in Figure 4. Generally, the lake became a more stressful system as the season progressed. Availability of inorganic carbon for photosynthesis decreased through the summer to limiting levels (King 1970). Water transparency decreased dramatically in early July and decreased more slowly till the end of the study. Phosphates and nitrates showed maximums in late July, then decreased slightly in August. Temperature and pH increases were slight.

Environmental stresses on the phytoplankton in the late summer had the effect of reducing biological and environmental diversity. Figure 5 summarizes diversity trends along the time continuum. Environmental variation decreased through the summer, essentially reducing the number of niches available to organisms. Species diversity (measured by the Shannon-Wiener index) and community variation (the evenness of the contribution made by each species) also decreased through the summer. The last point on the community variation curve is much higher than the overall trend, due to the fact that in August the algal communities were composed of approximately equal contributions of *Ceratium* and/or *Aphanizomenon*, which normally comprised over 90 percent of the algae in a given sample.

Simple regression analysis of individual species plotted against environmental gradients shows several significant relationships (Table 2). Species showing the same significant trends were grouped into units. The first two groups are essentially early summer species and are predominately green and blue-green algae. As expected,

TABLE 1. Mean standing crop values of Utah Lake algae in the summer of 1974 according to collection date.

Date	Mean number of organisms per liter
4 June	13,758
13 June	2,230
21 June	20,754
3 July	52,251
10 July	416,128
18 July	541,128
27 July	344,968
7 Aug.	724,061
15 Aug.	10,866,586

they generally correlate with environmental parameters that predominate in the early summer, such as high light penetration, free CO_2, and low water temperatures. *Aphanizomenon* and *Ceratium* correlate with environmental parameters that were prevalent in the latter part of the season (i.e., high turbidity, high salinity, high phosphates, basic pH, and higher temperatures). As mentioned previously, increase in temperature through the season was slight and, therefore, is probably not a causal relationship even though the correlation with *Aphanizomenon* and *Ceratium* was significant.

Discussion

Communities seldom appear as discrete units. In many cases closely allied communities intergrade one with another both in time and space and often exhibit no distinct boundaries between them. This is especially true of aquatic systems and in instances of biological succession. Therefore, the continuum theory as used in this paper is especially useful in the description of the algal communities of Utah Lake. The Curtis continuum has been traditionally used to describe the response of terrestrial vegetation to environmental gradients. However, the principle is just as applicable to aquatic systems where the species involved are mobile and succession is seasonal.

The Curtis continuum is also especially useful in environments that are highly fluid, as in the case of planktonic systems. Thus, we have noted in Utah Lake that certain geographical regions maintain early summer floras for more extended periods of time due to local environmental conditions which approximate earlier seasonal conditions. This was noted particularly in the Provo Boat Harbor and Goshen Bay, where spring and river influences are prominent.

Summer phytoplankton communities in Utah Lake are marked by decreases in diversity of the flora as the system becomes more stressed and/or uniform. The phytoplankton of June are a diverse assortment of species representing several algal divisions. Chlorophyta are important and are mainly associated with Cyanophyta and diatoms. The July phytoplankton are still a diverse group, but are predominately *Melosira granulata*, two species of *Anabaena*, and *Ceratium hirundinella*. The reduction of species

Table 2. Species correlation patterns with respect to environmental parameters as analyzed by regression analysis. Species with similar responses are grouped. All correlations listed are at the 0.01 significance level.

Species Clusters	Correlations: Positive	Correlations: Negative
Ankistrodesmus falcatus var. mirabilis Ankistrodesmus falcatus var. stipatus Dinobryon divergens Merismopedia glauca Holopedium irregulare Trebaria triappendiculata	Light penetration Free CO_2	Dissolved O_2 Conductivity Total alkalinity SiO_2
Anabaena flos-aquae Ankyra judayi Epizooites Microcystis incerta Pediastrum duplex Chlamydomonas globosa	Total alkalinity Calcium hardness	Water temperature Total hardness
Carteria stellifera Scenedesmus quadracauda	Total hardness	Nitrates Magnesium hardness
Aphanizomenon flos-aquae Ceratium hirundinella	Turbidity Salinity Phosphates pH Water temperature	

diversity to an almost exclusive *Aphanizomenon-Ceratium* community by August is probably due to competition, release of allelopathic substances by *Aphanizomenon* (Palmer 1962), and reduction of environmental niches due to decreased variability in the envirionment (Fig. 5).

Silica depletion to less than 0.5 mg/liter has been implicated as a factor that is often important in determining succession from diatom-dominated communities to blue-greens (Lund 1965). However, this is not the case in Utah Lake, where silica levels are very high (an average of 19.4 mg/liter for the summer and even higher in August).

Water temperature has been shown to be very important in influencing succession from diatom-dominated to blue-green-dominated floras (Patrick 1969). Apparently, this is not the case in Utah Lake. Water temperature is relatively constant throughout the study period and is highest in July when *Melosira* (the dominant diatom) is most abundant.

King (1970) has shown that, under conditions of low alkalinity and high pH, algae may be carbon limited. Blue-green algae seem to be most tolerant to these conditions and Chlorophyta seems to be most sensitive. In Utah Lake, there was a continuing decrease in available inorganic carbon (Fig. 6). The disappearance of most chlorophytes corresponds with the period of greatest decrease in carbon availability. In August, when most of the remaining algal species were replaced by *Aphanizomenon* and *Ceratium*, carbon stress was most severe. Many samples had a pH of 8.5 or more and carbonate alkalinity near 20 mg/liter. King's data (1970) indicate that these conditions are marginal for growth of assorted blue-greens used in his cultures. From this information, carbon limitation is probably an important factor in determining the composition of the summer phytoplankton communities in Utah Lake.

It is important to note that August communities in the Lake were dominated by *Aphanizomenon flos-aquae* and *Ceratium hirundinella*, which comprised between 89 and 100 percent of the total algal standing crop. These communities were often composed of only *Aphanizomenon* or *Ceratium* exclusively. We believe this is strong evidence that competitive exclusion is an important factor in regulating the late summer communities of Utah Lake. This hypothesis is presently under investigation in our laboratory.

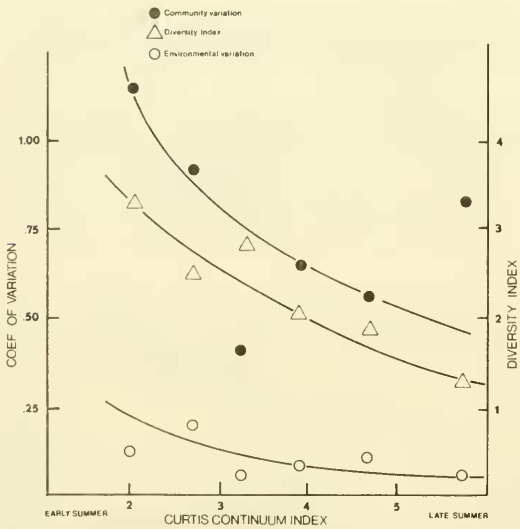

Fig. 5. Trends in species diversity, community variation, and environmental variation in Utah Lake in the summer of 1974, plotted on the Curtis continuum index.

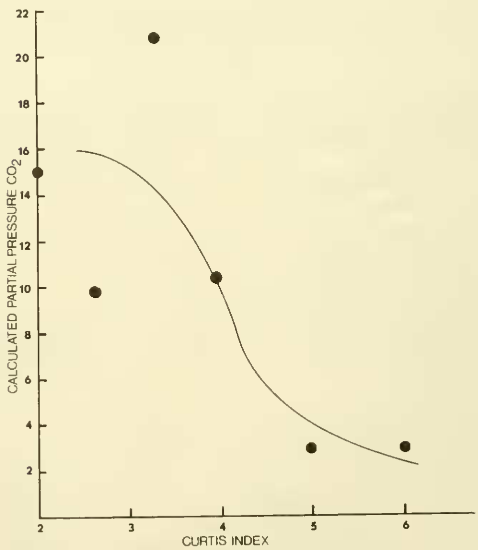

Fig. 6. Partial pressure of CO_2 in Utah Lake in the summer of 1974, calculated from disassociation constants plotted on the Curtis continuum index.

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